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Chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) quantify split solid objects

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Abstract Recent research suggests that gorillas' and orangutans' object representations survive cohesion violations (e.g., a split of a solid object into two halves), but that their processing of quantities may be affected by them. We assessed chimpanzees' (*Pan troglodytes*) and bonobos' (*Pan paniscus*) reactions to various fission events in the same series of action tasks modelled after infant studies previously run on gorillas and orangutans (Cacchione and Call in Cognition 116:193–203, 2010b). Results showed that all four non-human great ape species managed to quantify split objects but that their performance varied as a function of the non-cohesiveness produced in the splitting event. Spatial ambiguity and shape invariance had the greatest impact on apes' ability to represent and quantify objects. Further, we observed species differences with gorillas performing lower than other species. Finally, we detected a substantial age effect, with ape infants below 6 years of age being outperformed by both juvenile/adolescent and adult apes.

Keywords Core knowledge · Object representation · Cognitive development · Comparative cognition · Cohesiveness and continuity

Introduction

The core principle of cohesion (Spelke 1994; Spelke and Kinzler 2007) is the most fundamental defining property of the ontological category of objects (Bloom 2000; Pinker 1997; Scholl 2007). Core principles serve to build representations of and reason about ecologically important events and entities and are thus most likely shaped by natural selection and shared by various primate (and probably even other mammal) species (e.g., Cacchione and Call 2010a, b; Cacchione and Krist 2004; Cacchione et al. 2009; Mendes et al. 2008; Santos 2004). Recently, several studies confirmed that cohesion is fundamental to represent, track, and reason about persisting objects because human infants' and adults' as well as non-human primates' object representations are affected after the perception of cohesion violations (Cacchione and Call 2010b; Cheries et al. 2008; Chiang and Wynn 2000; Huntley-Fenner et al. 2002; Mitroff et al. 2004; Rosenberg and Carey 2006; van Marle and Scholl 2003). The impact of cohesion violations was assessed with different methodologies ranging from perceptual measures (i.e., the violation of expectation paradigm, perceptual object tracking studies) to action-based measures (i.e., forced choice crawling procedure, forced choice cup selection).

Particularly in human infants, perceiving the decomposition of a solid object (e.g., by breaking it in two or more pieces) had a major impact on their ability to represent its continuous existence (Cheries et al. 2008; Chiang and Wynn 2000). Chiang and Wynn (2000) compared with 8-month-old infants' reasoning about solid objects and

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collections of objects such as non-cohesive piles of objects (pyramids of blocks) in occlusion events using a violation of expectation procedure. Infants saw one or two objects moving behind a screen. The removal of the screen revealed either a consistent event (expected number of objects) or an inconsistent event (unexpected number of objects). Infants' looking times to the outcomes were compared to see, whether they detected the magical disappearance of some of the objects. When infants were presented with solid pyramids that maintained their boundaries throughout the whole event, they succeeded in this task (i.e., looked longer if one of the objects was missing). However, if infants first saw the decomposition of the pyramid into five blocks and then their rearrangement into a pyramid, they failed to track and individuate the objects. Later, Cheries et al. (2008) showed that even the most simple cohesion violation, the fission of a single solid object into two parts affected infants' ability to represent and quantify objects. He used the so-called forced choice crawling procedure where infants are presented with cups being baited with different cracker amounts. Infants are allowed to crawl to the cup of their preference (which in young infants is always the cup containing the greater amount of food). Infants presented with a single big cracker that was split into two halves before placing it into the cup failed to select the cup containing the greater amount (which is what they did in an identical condition without a splitting event). Obviously cohesion violations heavily affect infants' object representation at least up to the age of 16 month (see Cheries and Carey 2009); however, it is unclear why this is the case. It is possible that (a) infants conceive of split objects as of a *non-object* entity, (b) their object representation is fully destroyed by observing the cohesion violation, or (c) their initial representation survives the splitting, but is impaired and thus ineffective in comparative judgments (Cheries et al. 2008; Chiang and Wynn 2000). The last possibility is strongly supported by the findings on human adults and non-human primates using perceptual measures. Although adults' object representations were limited in their function when tracked objects split into two (Mitroff et al. 2004), their representation clearly survived the splitting. Similarly, Mahajan et al. (2009) reported that brown lemurs (*Eulemur fulvus*) successfully enumerated objects that were decomposed into multiple pieces in a violation of expectation paradigm.

Recently, Cacchione and Call (2010b) adopted the Cheries et al. (2008) forced choice methodology to investigate orangutans' and gorillas' reactions to five splitting events resulting in different amounts of non-cohesiveness according to the following ranking (from high to low): (1) smashing a cracker in one blow (transformed the solid cracker into a substance and thus into a "non-object entity") resulted in the highest degree of spatial ambiguity, the disassembly occurred in a very short time and the

original objects' shape was fully destroyed; (2) successively splitting the cracker in six small pieces also resulted in high spatial ambiguity and destroyed the shape of the original object, but the slow erosion facilitated the conservation of the object representation; (3) splitting the cracker into two halves resulted in comparatively low spatial ambiguity but affected the shape; (4) breaking off a small edge and (5) breaking out the centre of the cracker both produced a comparatively low spatial ambiguity and preserved the original object's shape (see Cacchione and Call 2010b for a more detailed account of how these manipulations result in different levels of cohesion). If object cohesion is the main factor fostering the representation (and quantification) of solid objects, these abilities should vary as a function of perceived object cohesion.

Cacchione and Call (2010b) found that the different splitting events affected apes' object representations but did not destroy them. Orangutans and gorillas were able to quantify crackers split into two identical halves or crackers eroding slowly over time. They showed even higher rates of success if the fission had a low impact on the objects' outer contour (i.e., break off one edge and break out the centre). Only if the cracker was fully fragmented (i.e., smashed) their quantifications eventually broke down. However, their performance in this condition substantially improved if the task demands were reduced by using a larger proportionate difference between quantities to be judged. Thus, the results strongly suggested that even strong incidences of fission did not fully destroy apes' object representations but limited their operational capability as it has been observed in human adults (Mitroff et al. 2004). This suggests that gorillas and orangutans also manage to represent and quantify split objects.

The present studies aimed at reinforcing and extending the original findings of Cacchione and Call (2010b) by testing bonobos and chimpanzees and consequently completing this data set in the great apes. To allow for a direct comparison between species, we tested chimpanzees and bonobos with exactly the same design and procedure as gorillas and orangutans in the original study. Would chimpanzees and bonobos, just like orangutans and gorillas, successfully represent and quantify split objects? The investigation of multiple species closely related to humans is of special interest to make strong inferences about the distribution and evolution of this important core feature of physical cognition. Specifically, potential species differences in great apes' vulnerability to cohesion violations would offer very important insights into the phylogenetic history of apes' capacity to perceive, represent, and reason about physical objects.

Further, we investigated whether nonhuman great apes' vulnerability to fission events also decreases during ontogeny (as it has been observed in human infants).

Combining the data of all four species in this paradigm created a sample size that enabled us to compare the performance of infants (0–5 years), juveniles and adolescents (6–14 years), and adults (15–35 years). Finally, we examined potential order effects in task administration. In the original study, baseline condition and split-in-halves condition were assessed first, followed by a set of four split conditions resulting in varying degrees of non-cohesiveness. This might have influenced apes performance (e.g., downgraded their performance in the conditions that were assessed first and vice versa). Thus, in the present study, we tested a second subsample with a fully counterbalanced design to assess potential order effects (Experiment 2).

Experiment 1

Methods

Participants

Twelve great apes (six chimpanzees [*Pan troglodytes*] and six bonobos [*Pan paniscus*]) participated in the study (Table 1). All apes were housed at the Wolfgang Köhler Primate Research Center (Leipzig zoo) in Germany. All had prior experience with various experiments investigating physical and social cognition. Four chimpanzees and four bonobos had prior experience with an investigation on quantity-based discriminations (see Hanus and Call 2007); three chimpanzees and four bonobos participated in an investigation on liquid conservation (see Suda and Call 2004). Apes were tested alone either in an indoor observation room or in their

sleeping room. Mothers with infants younger than 3 years of age were tested in the company of their offspring.

Materials

The stimuli were pieces of wheat crispbread. They measured 6 cm × 5.5 cm (*big* cracker, see Fig. 1 “initial presentation”), 3 cm × 5.5 cm, or 3 cm × 2.7 cm, respectively (*small* crackers, see Fig. 1 “comparison ratios 1:2 or 1:4”). To ensure that the single big cracker would split into two exactly identical halves, the desired breaking line was pre-carved on the backside of the cracker. This manipulation was not visible to the participants. The crackers were placed into two oblong opaque cups (9 cm diameter, 17 cm high). Once the cracker pieces were placed into the cups, the apes could not see them anymore.

Design and procedure

The ape sat behind a Plexiglas panel with two holes through which s/he could point. A testing surface (slide table) was fixed by a metal frame directly underneath the panel, and the two cups were placed on top of it (58 cm apart of each other) in front of the holes. The experimenter sat in front of the slide table, which was constructed such that its surface could be shifted back and forth. The experimenter pulled the table back and baited the cups in full view of the ape. Procedure and design were as described in Cacchione and Call (2010b). The apes were presented with two conditions, a split-in-halves condition and a baseline condition where the objects were not split (no-split condition). Each condition consisted of 1 session

Table 1 Age [years], sex [M = male, F = female] and distribution into the three age classes [1 = infant (0–5 years), 2 = juvenile/adolescent (6–14 years), 3 = adult (15–35 years)] of the participating subjects

| | Experiment 1/2 | | | | Experiment 2 | | | | Cacchione and Call (2010b) | | |
|--------------------|----------------|-----|-----------|--------------------|--------------|-----|-----------|-------------------|----------------------------|-----|-----------|
| | Sex | Age | Age class | | Sex | Age | Age class | | Sex | Age | Age class |
| <i>Bonobos</i> | | | | <i>Chimpanzees</i> | | | | <i>Orangutans</i> | | | |
| Joey | M | 26 | 3 | Robert | M | 33 | 3 | Bimbo | M | 28 | 3 |
| Limbuko | M | 14 | 2 | Frodo | M | 15 | 3 | Dunja | F | 35 | 3 |
| Kuno | M | 12 | 2 | Patrick | M | 12 | 2 | Pini | F | 20 | 3 |
| Kuno | F | 16 | 3 | Lome | M | 8 | 2 | Dokana | F | 19 | 3 |
| Yasa | F | 12 | 2 | Lobo | M | 5 | 1 | Padana | F | 10 | 3 |
| Luiza | F | 4 | 1 | Kofi | M | 4 | 1 | <i>Gorillas</i> | | | |
| <i>Chimpanzees</i> | | | | Fraukje | F | 33 | 3 | Bebe | F | 29 | 3 |
| Alex | M | 8 | 2 | Riet | F | 31 | 3 | Viringika | F | 13 | 2 |
| Alexandra | F | 10 | 2 | Natascha | F | 29 | 3 | Kibara | F | 4 | 1 |
| Annett | F | 10 | 2 | Dorien | F | 28 | 3 | | | | |
| Gertruida | F | 16 | 3 | Tai | F | 7 | 2 | | | | |
| Jahaga | F | 16 | 3 | Kara | F | 4 | 1 | | | | |
| Fifi | F | 16 | 3 | | | | | | | | |

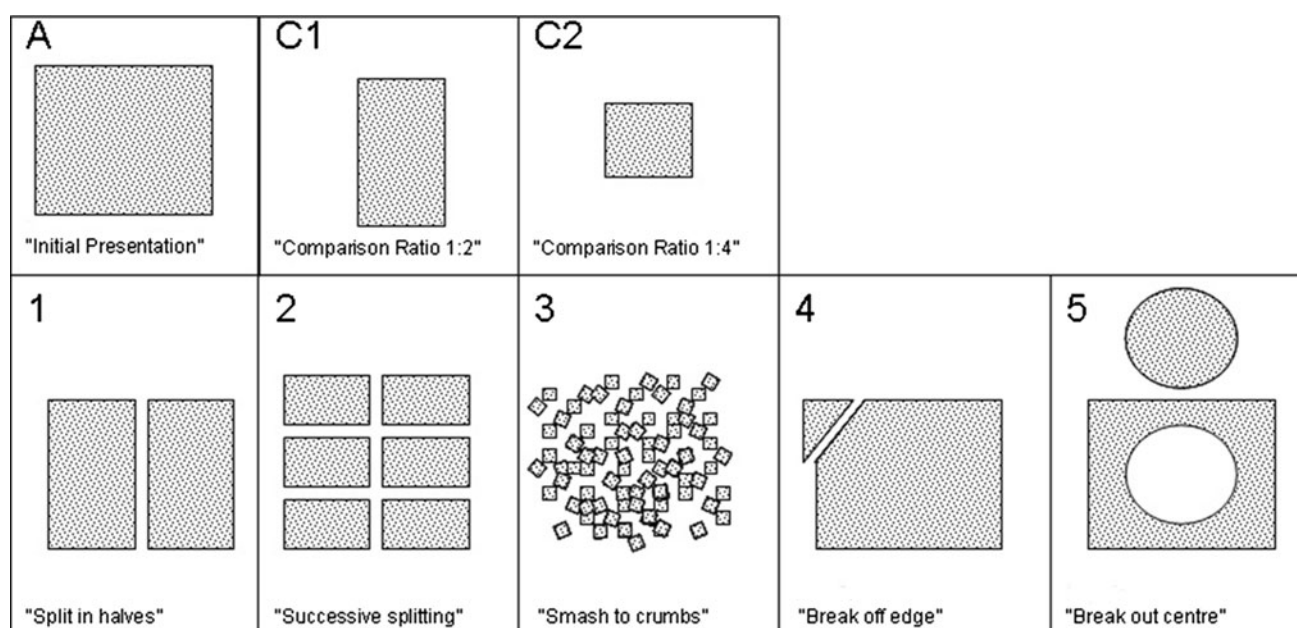


Fig. 1 Schematic depiction of stimuli used in Experiments 1–2

with 6 trials. In the split-in-halves condition, the experimenter held out a single big cracker (see Fig. 1, “initial presentation”) and broke it in two identical halves before placing it into a cup. The other cup was baited with a cracker of only half (comparison ratio 1:2) or a quarter (comparison ratio 1:4) of the size the original single big cracker. To prevent biasing the subject by stimulus enhancement, the smaller cracker amount was always handled in a similar manner (i.e., grasping it alternately with both hands) and for an equal amount of time before placing it into the cup. After the baiting, the experimenter pushed the sliding table to the panel. The ape could now point at the cup of his/her choice. The experimenter drew the table back again and handed over the content of the chosen cup to the ape. The no-split condition was identical to the split-in-halves condition, except that apes never witnessed the splitting, but they were directly presented with two identical cracker halves. The experimenter did not place the crackers into the cup unless the apes watched her doing so. Condition (split-in-halves condition and no-split condition), cup ratio (1:2 and 1:4), side (larger amount of food in the left or right cup), and order of presentation (larger amount of food placed first or second) were counterbalanced across participants.

Data scoring and analysis

We videotaped all trials and scored them live on coding sheets. A second observer scored a random sample of 20 % of the trials. Inter-observer reliability was high (index of concordance = .99, kappa = .98, $n = 116$). Data analysis

was done with Excel 2003 for Windows and SPSS 14.0, using nonparametric statistics.

Results

Apes selected the larger of two quantities above chance in all conditions (Wilcoxon test: split 1:2: $z = -3.103$; no-split 1:2: $z = -2.976$; split 1:4: $z = -3.274$; no-split 1:4: $z = -3.217$; $p < .01$ in all cases; Fig. 2). Overall, there was no significant difference between the split-in-halves condition and the no-split condition (Wilcoxon test: $z = -1.173$, $p = .241$). Similarly, there were no differences between conditions in the first trial (Sign test: 1:2: $p = .625$; 1:4: $p = 1.000$) and no differences between conditions within each ratio (Wilcoxon test: 1:2: $z = -1.174$, $p = .240$; 1:4: $z = -.378$, $p = .705$). However, apes performed reliably better for a cup ratio 1:4 (Wilcoxon test: $z = -2.675$, $p < .01$). Finally, there was no evidence of learning in the course of the conditions, assessed by comparing the first three trials with the second three trials (Wilcoxon test: split 1:2: $z = -.276$; no-split 1:2: $z = -.851$; split 1:4: $z = -1.342$; no-split 1:4: $z = -.577$; $p > .05$ for all cases).

Species comparisons

Comparing the overall performance of the chimpanzees and bonobos in the present study with the orangutans and gorillas of Cacchione and Call (2010b) revealed species differences in both test conditions (Kruskal–Wallis Test: split: $\chi^2 = 7.935$; no-split: $\chi^2 = 10.659$; $p < .05$, $df = 3$ in both cases). These differences were due to the lower performance of gorillas in

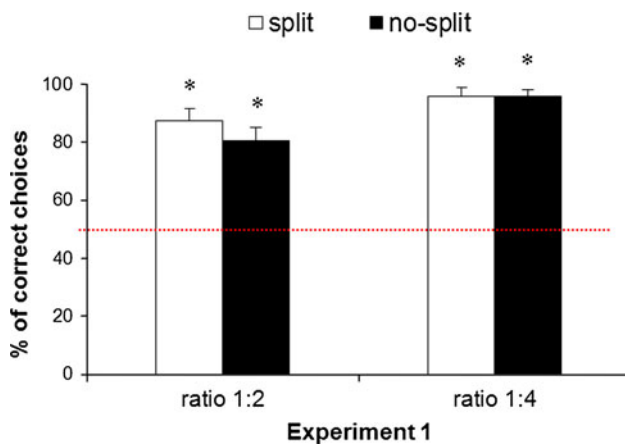


Fig. 2 Per cent of correct choices in Experiment 1 (“no-split” and “split-in-halves” conditions), for cup amounts differing by a ratio 1:2 and 1:4

the split condition as compared to orangutans (Mann–Whitney U test: $z = -2.249$, $p < .05$), and to the lower performance of gorillas in both split and no-split conditions as compared to chimpanzees (Mann–Whitney U test: split: $z = -2.364$; no-split: $z = -2.384$; $p < .05$ in both cases) and to bonobos (Mann–Whitney U test: split: $z = -2.364$; no-split: $z = -2.092$; $p < .05$ in both cases).

Discussion

Chimpanzees and bonobos were able to represent and quantify amounts of solid objects that were split into two halves. That is, as was earlier observed in gorillas and orangutans, their object representations clearly survived fission-type cohesion violations. Moreover, chimpanzees and bonobos even showed higher rates of correct performance than gorillas. The next experiment investigated chimpanzees’ and bonobos’ reactions to variants of fission events that either increased or decreased an object’s non-cohesiveness as compared to a split in halves. Again their responses were compared to the orangutans and gorillas of the original study. Additionally, we assessed age effects by comparing the performance of different ages. Finally, a sample of chimpanzees was tested with all the conditions of Experiments 1 and 2 in a fully counter-balanced order to investigate potential order effects.

Experiment 2

Methods

Participants and materials

The same great apes as in Experiment 1 also participated in Experiment 2. Additionally, a sample of 12 naïve

chimpanzees was tested with the conditions counterbalanced (Table 1). All had prior experience with various experiments investigating physical and social cognition. Five had prior experience with an investigation on quantity-based discriminations (see Hanus and Call 2007); one had participated in an investigation on liquid conservation (see Suda and Call 2004). Again all materials were made out of pieces of crispbread. In addition to the two opaque cups, one transparent cup was used to present the cracker after the smash manipulation (before filling it into the opaque cup, see below).

Design and procedure

Again design and procedure were the same as in Cacchione and Call (2010b). Apes were confronted with two cups. In one cup, the experimenter filled the big cracker that was manipulated/split. The second cup was baited with a cracker of only half (comparison ratio 1:2) or a quarter (comparison ratio 1:4) of the size the original big cracker (see Fig. 1). Instead of splitting the single big cracker into two identical halves, the apes now were presented with four new types of splitting manipulations producing varying degrees of non-cohesiveness (from high to low; see Fig. 1): (1) smashing the cracker into crumbs, (2) successively splitting the cracker in six parts, (3) breaking out of the centre of the cracker, and (4) breaking off one small edge of the cracker (see Fig. 1). In the smash condition, the experimenter held out the single big cracker (see Fig. 1, “initial presentation”) and then crushed it by closing her hand. Then, she opened the hand again and filled the resulting cracker crumbs into a transparent cup. After that she poured the content of the transparent cup in full view of the ape into the opaque cup. In the succession condition, the experimenter held out a big cracker and successively broke it into six small pieces. Each of the pieces was directly placed into the cup after it was broken off the original cracker. Thus, the cracker appeared to be gradually melting down. In the centre condition, a circle was broken out of the centre of the big cracker. Thus, the cracker was again split into two halves, but the outer contour remained unchanged. In the edge condition, only a small edge was broken off the big cracker. Again, in contrast to the split-in-halves condition of Experiment 1, the original cracker largely preserved its shape through the fission event. To prevent effects of stimulus enhancement, the smaller cracker amount was handled in a similar manner (i.e., grasping it alternately with both hands) and for an equal amount of time before placing it into the cup.

All apes received two blocks (ratio 1:2 and ratio 1:4) with four conditions. All apes first received a block with a ratio 1:4 followed by a block with a ratio 1:2. Over both blocks, the conditions were administered in a quasi-randomized fashion (e.g., block 1: edge-centre-succession-

smash; block 2: smash-succession-centre-edge). Each condition consisted of six trials. Again side and order of presentation were counterbalanced across participants.

Additionally, a sample of 12 chimpanzees was tested with all the events of Experiments 1 and 2 in a fully counterbalanced manner. They too were presented with two ratio blocks (ratio 1:2 and 1:4) and six conditions (joint Experiments 1 and 2) but the order of conditions and ratios were fully counterbalanced among the participants. It is possible that the order of conditions influenced apes' performance in the original design in that they might have performed better in conditions they received later because they acquired learning set experience. We hypothesized thus that if the order of conditions affected the performance, apes receiving the fully counterbalanced design should perform (1) higher in the split and no-split conditions, (2) lower in the centre, edge, succession, and smash conditions, and (3) higher in tasks with a ratio 1:4 than the apes of the original design.

Results

Figure 3 presents the percentage of trials in which subjects selected the larger quantity of crackers. Apes failed to select the larger quantity in the smash condition when cups differed by a ratio 1:2 (Wilcoxon test: $z = -1.469$, $p = .142$). However, they chose above chance level in all other conditions (Wilcoxon test: smash 1:4: $z = -3.357$; succession 1:2: $z = -2.873$; succession 1:4: $z = -3.357$; edge 1:2: $z = -3.274$; edge 1:4: $z = -3.464$; centre 1:2: $z = -3.274$; centre 1:4: $z = -3.464$; $p < .01$; see Fig. 3).

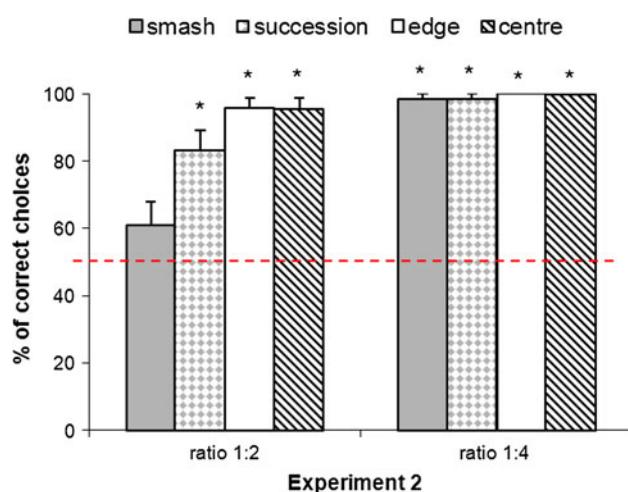


Fig. 3 Per cent of correct choices in Experiment 2 (“successive splitting”, “smash to crumbs”, “break off edge” and “break out centre” conditions) for cup amounts differing by a ratio 1:2 and 1:4

Effects of condition: overall performance

Overall, apes' performance across conditions reliably differed (Friedman test: $\chi^2 = 22.06$, $df = 3$, $p < .001$, $N = 12$). Apes performed reliably better in the succession condition, the centre condition, and the edge condition than in the smash condition (Wilcoxon test: succession: $z = -2.143$; edge: $z = -2.770$; centre: $z = -2.821$, $p < .05$ in all cases). Also, apes performed better in the centre and edge conditions than in the succession condition (Wilcoxon test: $z = -2.041$, $p < .05$ in both cases) while their performance in the centre and edge condition did not differ (Wilcoxon test: $z = 0$, $p = 1.0$). In general, apes performed reliably better in both events with decreased non-cohesiveness than in the split-in-halves condition of Experiment 1 (Wilcoxon test: $z = -2.207$, $p < .05$ in both cases). However, comparing events with increased non-cohesiveness to the split-in-halves condition of Experiment 1 revealed that apes only performed reliably lower in the smash condition but not in the succession condition (Wilcoxon test: smash: $z = -2.138$, $p < .05$; succession: $z = -.140$, $p = .888$).

Effects of condition: performance within each ratio

Also within a ratio 1:2, apes' performance differed between conditions (Friedman test: $\chi^2 = 22.06$, $df = 3$, $p < .001$, $N = 12$). This difference was not apparent for a ratio 1:4 (Friedman test: $\chi^2 = 2.00$, $df = 3$, $p = .572$, $N = 12$).

Effects of condition: first trial performance

There was a reliable difference in the first trial between the centre and smash conditions when cup amounts differed by a ratio 1:2 (Sign test: $p < .05$). In all other cases, there were no differences between conditions in the first trial (Sign test: $p > .07$ in all cases).

Effects of ratio

The apes overall reliably more often selected the larger amount for a ratio 1:4 (Wilcoxon test: $z = -2.952$, $p < .01$).

Training effects

There was no evidence that subjects improved performance during testing assessed by comparing the first three trials with the second three trials (Wilcoxon test: succession 1:2: $z = -.949$; succession 1:4: $z = -1.000$; smash 1:2: $z = -.241$; smash 1:4: $z = -1.000$; edge 1:2: $z = -.447$; edge 1:4: $z = .000$; centre 1:2: $z = 1.000$; centre 1:4: $z = .000$; $p > .05$ in all cases).

Species comparisons

Comparing the overall performance of chimpanzees and bonobos in the present study with the orangutans and gorillas revealed species differences in the smash and the edge conditions (Kruskal–Wallis Test: smash: $\chi^2 = 8.987$; edge: $z = 7.912$; $p < .05$, $df = 3$ in both cases). These differences were mainly due to gorillas' lower performance in the edge condition as compared to chimpanzees (Mann–Whitney U test: $z = -2.121$, $p < .05$) and orangutans' and chimpanzees' lower performance in the smash condition as compared to bonobos (Mann–Whitney U test, orangutan/bonobo: $z = -2.592$; chimpanzee/bonobo: $z = -2.445$; $p < .05$ in both cases).

Age effects

There were age differences in the split-in-halves, the no-split, the centre and the edge conditions (Kruskal–Wallis Test, split: $\chi^2 = 6.023$; no-split: $\chi^2 = 8.305$; centre: $\chi^2 = 6.690$; edge: $\chi^2 = 9.570$; $p < .05$, $df = 2$ in all cases), whereas performance did not differ in the smash and in the succession condition (Kruskal–Wallis Test: smash: $\chi^2 = .222$; succession: $\chi^2 = 3.151$, $p > .05$, $df = 2$) (see Fig. 4). Infants performed worse than juveniles (Mann–Whitney U test: split: $z = -2.330$; no-split: $z = -2.974$; centre: $z = -2.616$; edge: $z = -3.118$; $p < .05$ in all cases) and adults (Mann–Whitney U test: split: $z = -2.007$; no-split: $z = -2.305$; edge: $z = -2.198$; $p < .05$ in all cases). In contrast, the performance of juveniles and adults did not differ. Nevertheless, infants still performed above chance in all conditions (Wilcoxon test: split: $z = -2.032$; no-split: $z = -2.023$; smash: $z = -2.023$; succession: $z = -2.032$; centre: $z = -2.032$; edge: $z = -2.070$; $p < .05$ in all cases).

Order effects

We compared the performance of the chimpanzees with the fully counterbalanced design with the chimpanzees of the

original design ($n = 6$). Comparing the overall performance of the two samples tested with different designs (original design vs. fully counterbalanced design) revealed that chimpanzees tested with the fully counterbalanced design performed reliably lower in the edge condition (Mann–Whitney U test: edge: $z = -2.501$; $p < .05$) but reliably better in conditions where cup amounts differed by a ratio 1:4 (Mann–Whitney U test: $z = -2.133$, $p < .05$). In all other conditions/ratios, they did not differ.

Discussion

Apes generally performed well in all test events. They performed above chance in all conditions except in the smash condition where they failed to quantify amounts of a cracker that was smashed into crumbs before filling it into the cup. However, this effect was only observed if cup amounts differed by a ratio 1:2, but not in the easier 1:4 version of the task. In the smash condition, the cracker piece was fully fragmented, and fragmentation occurred in a very short time period, both factors handicap the conservation of the object representation through fission. However, even in the face of this strong interference, apes' representations were not fully destroyed, since the apes succeeded with a ratio 1:4. Although performing well, apes' performance was obviously influenced by the degree of non-cohesiveness produced in the different splitting events. This confirms that apes' ability to represent and quantify may indeed be affected by fission events. Further, also in the present study, the proportionate ratio between cup contents influenced apes' behaviour which confirms the previous finding that quantity judgements involving higher ratios are more difficult to solve for great apes and other non-human primate species (Addessi et al. 2008; Beran 2001, 2004, 2010; Beran and Beran 2004; Beran et al. 2009; Hanus and Call 2007; Lewis et al. 2005; van Marle et al. 2006).

Overall, chimpanzees and bonobos tested in the present study performed similar as the orangutans and gorillas tested in Cacchione and Call (2010b). Just like orangutans and gorillas, chimpanzees and bonobos also performed best if the splitting had only low impact on object cohesion (e.g., edge, centre) and worst if the splitting heavily violated object cohesion (e.g., smash). Moreover, their performance in the split-in-halves and the succession conditions was intermediate. Again, we observed some species differences, most of them were connected to the lower performance of gorillas in contrast to the other 3 species tested. Furthermore, we observed substantial age differences with infants performing reliably worse than juveniles/adolescents and adults. Infants performed worse than the other two age groups in the majority of tasks (including the no-split baseline). One exception was the

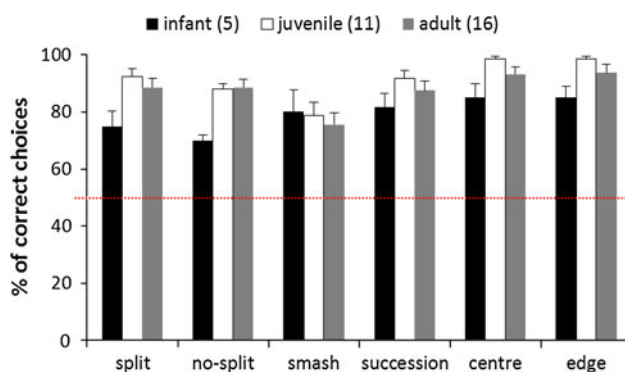


Fig. 4 Comparison of the performance of the three different age classes (numbers in parentheses indicate the number of participants in each age class)

two split events that produced the most non-cohesiveness. These differences are further addressed in the general discussion.

Finally, comparing the performance of chimpanzees tested either with the original or with a fully counterbalanced design revealed overall performance differences in the edge condition and for a 1:4 ratio. The better overall performance of the fully counterbalanced group in the edge task and their lower performance for a 1:4 ratio might be a consequence of test order effects in the original design. Thus, at least in these two cases, order effects may have contributed to the good performance of apes tested with the original design. However, both samples of chimpanzees performed over 90 % correct in the edge task and thus showed higher rates of success than in all other conditions. Likewise, both samples of chimpanzees performed over 90 % correct for a 1:4 ratio and thus better than for a 1:2 ratio. This suggests that even if the original design very slightly overestimated the succession rate of the apes in these cases, the overall performance pattern was the same.

However, there is one important alternative explanation that must be ruled out. It is possible that the apes found the highly damaged cracker in the smash 1:2 condition simply less appealing. In this case, apes might have been perfectly able to quantify the smashed cracker, but did nevertheless fail to select the bigger amount, because of an intrinsic preference for undamaged (whole) crackers.

Experiment 3

Under specific circumstances, apes have been found to depart from the usual food maximizing rule and show a preference for smaller whole amounts over larger fractionated amounts of food (see e.g., Beran et al. 2009). To rule out the possibility that apes' performance in the smash 1:2 ratio is best explained by apes' preference for a smaller (ratio 1:2) but not a too small (ratio 1:4) whole cracker over a larger highly fragmented cracker, we ran the following control. Apes were presented with a large cracker that was inserted into an accurately fitting square plastic form. The experimenter then smashed the cracker by repeatedly pressing her fingers (index and thumb) on it. Although the cracker was obviously highly fragmented, it preserved its' original form (i.e., the remaining pieces were held in shape by the plastic form). Thereby, we kept effects on the crackers' cohesion low. A second similar form was filled with a cracker of only half the size. The cracker amounts were not covered but presented in full view (in order to rule out effects of representation). If apes simply had an intrinsic preference for the undamaged cracker in the smash ratio 1:2 condition, they should again fail to select the larger cracker above chance level.

Methods

Participants and materials

Five chimpanzees and five bonobos that already participated in Experiments 1 and 2 also participated in Experiment 3 (two additional apes could not be tested: Limbuko moved to a new housing; Annett failed to participate in the test; see Table 1).

Design and procedure

The procedure was identical to the one used in the main test conditions, except that the cracker amounts were not covered but presented in full view.

Results and discussion

Apes chose the larger damaged cracker in 77 % of trials (Wilcoxon test: $z = -2.345$, $p < .05$). This is marginally different from their performance in the smash 1:2 condition (Wilcoxon test: $z = -1.869$, $p < .06$) and suggests that the apes do not generally avoid smashed crackers for a ratio 1:2 comparisons. Thus, if the effects on shape are kept low and apes must not compare the cup amounts on the base of their representations, they successfully quantify also highly damaged crackers. However, the comparatively low performance in this task indicates that a weak tendency to avoid highly fragmented crackers may be present in the apes. Although this tendency appears too weak to explain the observed response pattern in the smash ratio 1:2 condition, it cannot be excluded that it exacerbated apes' already low performance.

General discussion

Chimpanzees and bonobos were able to quantify split solid objects in the context of various fission events. They were able to quantify crackers split into two identical halves, crackers eroding slowly over time and they performed even better if only a small edge was broken off or the centre was broken out of the original cracker. This confirms the findings of the Cacchione and Call (2010b) study and broadens the empirical base for the claim that great apes' object representations are highly robust in the context of fission events. Similar to brown lemurs and 16-month-old human children, but unlike 12-month-old human infants, great apes represent and quantify a solid cracker that was split into two halves. In contrast to brown lemurs (Mahajan et al. 2009), great apes were tested with an action design modelled after the infant study of Cheries and Carey (2009) and their performance is thus directly comparable to findings in human infants.

Moreover, the present study confirms the finding that great apes' ability to represent and quantify split solid objects varies as a function of non-cohesiveness produced by the different splitting events. Apes were more likely to correctly assess quantities in fission events with a low impact on object cohesion (e.g., centre and edge conditions), whereas they had greater difficulty to correctly judge quantities if the splitting heavily affected object cohesion (e.g., smash). The main reason why centre and edge conditions posed the lowest difficulty on apes' quantification was likely their low impact on the objects outer contour (i.e., boundedness). In both cases, the objects shape was almost unaffected. Further, in both cases, the split resulted in only two objects, and thus, spatial ambiguity was comparably low. In contrast, smashing the cracker posed the greatest challenge to apes' ability to represent and quantify because the splitting fully destroyed the shape of the object and resulted in many small parts which increased the spatial ambiguity. Thus, spatial ambiguity and shape invariance were the two dimensions with the greatest impact on apes' ability to represent and quantify objects in the present study. Both factors increase non-cohesiveness and produce high cost for the ability to track objects (Chiang and Wynn 2000; van Marle and Scholl 2003). Only little evidence was found for a further factor potentially affecting apes' performance in the present study. While earlier investigations found an intrinsic preference for undamaged (whole) crackers in events where cup amounts do not strongly differ, this tendency did not reliably influence apes cup selection in the present study. If the effects on shape were kept low and there was no need to compare the cup amounts on the base of their representation, apes succeeded in quantifying also highly damaged crackers for a ratio 1:2. Although a tendency to avoid smashed crackers may have contributed to apes' low performance in the smash condition, this tendency was evidentially not substantial enough to explain their failure in the smash 1:2 condition.

Apes' object representations never broke down completely. The apes never lost object permanence after experiencing cohesion violations, and when the task demands were reduced (i.e., tasks involving a larger proportionate difference), they even managed to quantify a strongly fragmented cracker. A fully counterbalanced design suggests that the original design may have slightly overestimated apes' success rate in the edge task and for a 1:4 ratio, but corroborates a basic overall performance pattern. Taken together, these findings confirm the results of Cacchione and Call (2010b) that even strong incidences of fission do not destroy apes' object representations but most likely limit their processing capacity as it has also been shown in human adults (Mitroff et al. 2004).

We observed some species differences, most of them connected to the lower performance of gorillas in contrast

to the other species tested, a pattern that has also been observed in other cognitive tasks (e.g., Amici et al. 2008). Other tasks, however, have not found a clear difference between gorillas and the other great apes. For instance, gorillas are as proficient as the other apes using tools (e.g., Girndt et al. 2008; Mulcahy et al. 2005) or making inferences about the location of objects (Call 2007; Mendes et al. 2008). Tasks on object individuation or object permanence are particularly interesting in connection to the current results because they rely on subjects' ability to track object identity despite spatio-temporal transformations (Scholl 2007). In such tasks, unlike the results of object fission, no clear-cut species differences have been detected.

We also observed substantial age effects on performance, with infants below 6 years of age being outperformed by both juveniles/adolescents and adults. However, age differences disappeared in the two splitting events that produced the most non-cohesiveness (smash and succession), an outcome due to the older apes' poor performance in those conditions. How does this compare to the ontogenetic shift that is observed in human infants from 12 to 16 months of age? Recall that 12-month-olds fail to quantify a cracker that was split into two identical halves, whereas 16-month-olds succeed. Thus, both human and nonhuman great apes seem to undergo an ontogenetic shift in object cognition. However, in contrast to 12-month-old human infants, the youngest apes did not totally fail to quantify the crackers after fission. But the youngest apes tested were 4 years old, which is about the youngest age that can be tested when multiple conditions are presented in succession. This means that we do not know how even younger apes would react, for example, whether they would also completely fail to quantify split crackers. Further, in contrast to human infants, young apes also performed relatively poorly in a condition where no splitting occurred (no-split condition). It is thus possible that the observed improvement over time has its roots in a general increase of attentional and executive control rather than more specifically focused on a vulnerability to fission. Additional research is needed to better understand these developmental changes.

In sum, the present findings confirm that while cohesion violations may affect apes' representational abilities, they do not destroy their representations of persisting objects. Instead, the impact of fission on the representation of solid objects is a function of their power to increase non-cohesiveness and mainly connected to degree of resulting spatial ambiguity and the extent to which the shape of the original object is changed through fission. As in humans, we also observed an ontogenetic shift with juveniles and adults outperforming infants below 6 years of age. However, future research must further explore why this shift

occurs in great apes and whether it is (as it is in human infants) connected to the decrease of vulnerability to fission events during cognitive development.

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